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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Marine subsidies likely cause gigantism of iguanas in the Bahamas

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Abstract

We utilized natural experiment opportunities presented by differential conditions (presence/absence of seabirds and invasive species) on cays in the Bahamas to study whether interisland variations in food resources contributed to gigantism in Allen Cays Rock Iguanas (*Cyclura cychlura inornata*). We analyzed the stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values from iguana tissues and resources from each island food web to test the predictions that (1) food webs on islands with seabirds exhibit the influence of marine subsidies from seabird guano, whereas those from non-seabird islands do not, and (2) size differences in iguanas among cays were due to either (a) supplemental food availability from mice and/or seabird carcasses killed by barn owls (*Tyto alba*) and/or (b) access to more nutrient-rich vegetation fertilized by seabird guano. Food web components from the seabird island (Allen Cay) had 5–9‰ higher δ^{15}N values than those on the other cays and Allen Cay plants contained nearly two times more nitrogen. Bayesian stable isotope mixing models indicated that C_3 plants dominated iguana diets on all islands and showed no evidence for consumption of mice or shearwaters. The iguanas on Allen Cay were ~ 2 times longer (48.3 ± 11.6 cm) and ~ 6 times heavier (5499 ± 2847 g) than iguanas on other cays and this was likely from marine-derived subsidies from seabird guano which caused an increase in nitrogen concentration in the plants and a resultant increase in the δ^{15}N values across the entire food web relative to non-seabird islands.

Keywords Stable isotope analysis · Allochthonous inputs · Audubon's Shearwaters (*Puffinus ihermineiri ihermineiri*) · Allen Cays Rock Iguana (*Cyclura cychlura inornata*) · Invasive species

Introduction

Significant body size differences observed in insular vertebrates, namely tendencies toward gigantism or dwarfism, are known as "The Island Rule" (Van Valen 1973) and its universality and causality have long been debated (Lomolino 1985; McClain et al. 2012; Meiri 2007; Meiri et al. 2006, 2008, 2011, 2012; Raia and Meiri 2006). Multiple mechanisms have been postulated as potential drivers of island gigantism (Case 1978; Durst and Roth 2015; Lomolino 1984; Meiri 2007; Michaux et al. 2002; Runemark et al. 2015), and we sought to understand the primary cause of extreme size divergence across populations of Allen Cays Rock Iguanas (*Cyclura cychlura inornata*) on islands in the Bahamas.

Three mechanistic explanations for insular gigantism in lizards are (a) release from predation (Runemark et al. 2015), (b) decreased intraspecific competition for resources experienced by individuals because of low initial densities in founder populations (Meiri 2007), and (c) availability of different food resources (Runemark et al. 2015). The Allen

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K. Richardson's novel contribution to the Island Rule literature provides mechanistic evidence of insular gigantism caused by marine subsidies with applications to the wider field of community ecology.

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Cays Rock Iguanas have no natural predators except herons that prey on very small juveniles throughout the Cays; so, predation risks were the same across our study islands (Iverson, personal observation), and thus, we rejected the first hypothesis. West Indian Iguanas can grow rapidly when first introduced in low densities to islands, but not at the scale we observed. For example, one out of eight *C.c. inornata* translocated as subadults in 1988 and 1990 from Leaf Cay to Alligator Cay in the Exuma Cays Land and Sea Park (for protection), quickly grew to 50 cm SVL (Knapp 2001), whereas the largest male among 5648 captures on Leaf Cay over 38 years measured only 49 cm SVL (Iverson et al. 2004b, unpublished). Similarly, two individuals of unknown size introduced to Flat Rock Reef Cay (FRRC; previously uninhabited) from U Cay in the mid-1990s grew to 46 cm SVL by 2001 (and measured the same in 2017; Iverson unpublished) and 44 cm by 2005 (46 cm SVL in 2010 at last capture; Iverson unpublished), respectively. Another Bahamian iguana, *C. rileyi nuchalis*, also translocated to a new island, grew to maximum size of 37 cm SVL ($n = 319$ captures) compared to a maximum of only 31 cm in the source population ($n = 52$ captures) (Hayes et al. 2004; Iverson et al. 2016). In these cases, iguana body size increased rapidly under low-density conditions. However, these 10–20% increases were substantially less than we observed for the unusually large iguanas in our study; so, decreased intraspecific competition cannot be the lone explanation. Therefore, to investigate our third hypothesis, we quantified potential differences in the quality of dietary resources available to these iguanas across islands.

Marine subsidies, when added to coastal terrestrial systems, usually via deposition by seabirds through guano, carcasses, and food scraps, can greatly enhance primary and secondary production, strongly regulate terrestrial food webs, and provide consumers with better quality food sources. Seabird guano is rich in nitrogen and phosphorous, both commonly limiting nutrients in terrestrial systems (Anderson et al. 2017). The deposition of seabird guano affects terrestrial productivity, increases the nutritional quality of land plants, fosters more complex trophic interactions, and increases trophic transfers in a system (Anderson and Polis 1999; Barrett et al. 2005; Ellis 2005; Havik et al. 2014; Kolb et al. 2012; Maron et al. 2006; Polis et al. 1997; Polis and Hurd 1996; Sanchez-Pinero and Polis 2000).

One tool to better understand food webs and the mechanisms contributing to trophic processes is stable carbon ($^{13}C/^{12}C$ or $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$ or $\delta^{15}N$) isotope analyses of food web components (Ben-David and Flaherty 2012). Stable nitrogen isotope values from consumer tissues provide a reliable indicator of trophic position as bulk $\delta^{15}N$ values increase predictably with increasing trophic level (Kurle et al. 2014). They are also used to trace marine subsidies into terrestrial food webs as seabird guano has elevated $\delta^{15}N$ values due to the high trophic level at which seabirds forage (Hobson et al. 1994). Also, the process of ammonia volatilization causes ^{15}N-enrichment in soil exposed to seabird guano, which is reflected in the $\delta^{15}N$ values of plants grown in that soil (Mizutani et al. 1985). Stable carbon isotope values act as indicators of food origin as $\delta^{13}C$ values vary with carbon sources and method of carbon processing (Boecklen et al. 2011).

We utilized stable isotope analyses and natural comparison opportunities across islands in the Bahamas (islands with and without Audubon's shearwater (*Puffinis iherminieri*) colonies, and invasive mice (*Mus musculus*) and barn owls (*Tyto alba*)) to examine (a) the trophic ecology of the Allen Cays Rock Iguana on islands with and without gigantism and (b) the mechanism(s) driving the observed interisland iguana size differences. We had two potential, trophic-related, mechanistic hypotheses. First, *C. c. inornata* is recognized as herbivorous (Iverson 1982), but true herbivory is found in only ~ 2% of lizard species worldwide (Iverson 1982; Pough 1973), and opportunistic foraging on animal matter has been observed within the genus *Cyclura* (Auffenberg 1982; Hines 2016; Iverson 1979; Luther et al. 2012). In addition, studies show that increasing protein content of diet increases growth rates and sizes of reptiles (Allen et al. 1989; Avery et al. 1993; Donoghue 1994; Donoghue et al. 1998; Mayhew 1963). Thus, we hypothesized that the interisland size differences observed in the Allen Cays Rock Iguanas could be explained by their ingestion of animal protein (mouse and/or shearwater carcasses) only available on one island (Allen Cay). Alternatively, consumers, including reptiles, on islands with access to better quality forage resulting from deposition of marine-derived nutrients are known to exhibit higher growth rates and increased body sizes and reach higher population levels than their conspecifics on neighboring sites lacking marine subsidies (Briggs et al. 2012; Pafilis et al. 2009, 2011; Ruffino et al. 2013; Sale and Arnould 2012). Thus, marine subsidies, only available via the shearwater colony on Allen Cay, may have caused the gigantism we observed in that iguana population.

Specifically, we analyzed the $\delta^{13}C$ and $\delta^{15}N$ values from producers and consumers within the islands' food webs and measured total nitrogen content of island plant material, to test the predictions that (1) the food web on the island with seabirds (Allen Cay) exhibited the influence of marine-derived nutrient subsidies, whereas the food webs from the other three cays did not, and (2) potential interisland iguana size differences were due to either (a) supplemental food availability from invasive mice and/or shearwater carcasses, and/or (b) access to more nutrient rich vegetation as a result of regular fertilization of plants by marine subsidies. Evidence to support predictions 1, 2a, and 2b would include: (1): The %N from the plants and the $\delta^{15}N$ values from the plants and consumers on Allen Cay would be significantly

Fig. 1 Map of Allen Cays, The Bahamas (24°45′N76°50.5′W). The four study Islands were Allen, Leaf, Flat Rock Reef (FRRC), and U Cay

Table 1 Size and seabird nesting status of islands with populations of *C. c. inornata* in this study (Iverson et al. 2006, Alifano 2011). *FRRC* Flat Rock Reef Cay

Cay	Size (ha)	Seabird category
Allen	6	High-density nesting; shearwaters, gulls
FRRC	5.3	Low-density nesting; gulls
Leaf	4	Non-bird
U	3	Very low-density nesting; shearwaters, gulls[a]

[a]There are no published reports for nesting shearwaters on U Cay and females on nests and carcasses are observed irregularly (J. Iverson, Personal Observation)

higher than those from plants and consumers on the other Cays, (2a) the δ^{15}N values from iguanas on Allen Cay would be higher than those of the shearwaters and mice by ~ 3 to 5‰ and much higher than those of the iguanas on all other Cays, and (2b) the δ^{15}N values from all plants and consumers on Allen Cay would be higher than those from the iguanas and plants on the other Cays, but the δ^{13}C and δ^{15}N values from iguanas would reflect consumption of primarily plant material and not mice or shearwaters.

Methods

Study sites, species, and history of species interactions

Our four study sites were three of the Allen Cays (Leaf, U, and Allen) and nearby Flat Rock Reef Cay (FRRC) in the Exuma Island Chain of the Bahamas (Fig. 1, Table 1). The Allen Cays Rock Iguana regularly feeds in bushes and trees (Knapp et al. 2004) and is endemic only to Leaf and U Cays (Schwartz and Carey 1977). However, the arrival of iguanas to Allen Cay and FRRC likely occurred via natural and human-mediated means in the past (Hines and Iverson 2006; Iverson 2012; Iverson et al. 2006, 2011; Knapp 2001). Genetic analysis of the iguanas on Allen Cay indicates that their source population is likely from Leaf Cay (Aplasca et al. 2016) and migration across the small channel separating Leaf and Allen Cays (see Fig. 1) is likely, especially given that hatchlings are known to migrate across open water channels between islands in the Andros Archipelago in the Bahamas (Knapp, Personal Communication to Iverson). There is no nesting habitat on Allen Cay, precluding their population growth via reproduction and the population was at ~ 20 to 25 individuals for several decades (Iverson, Personal Observation). Leaf Cay has the largest population of iguanas (~ 600), followed by U Cay (~ 300), FRRC (~ 200), and Allen Cay, which had 18–22 individuals in 2011 (Iverson et al. 2006). No formal vegetation surveys exist for these cays; however, plant species composition is roughly equivalent among the four study islands (Alifano et al. 2012; Iverson et al. 2004a).

C. c. inornata is listed as endangered on the IUCN Red List (Knapp et al. 2004), and is protected under CITES (Blair 2000). They face a multitude of threats, including tourist feeding and relocation (Hines 2011; Iverson et al. 2004b, 2011; Knapp et al. 2013), hunting (Knapp et al. 2004), invasive species introductions (Iverson et al. 2004b; Mackin 2007), and, due to its limited range, extreme vulnerability in the case of stochastic events (Knapp 2001; Richman et al. 1988).

The unique species assemblage on Allen Cay sets it apart from the other study sites as it contains the second largest breeding population of Audubon's Shearwaters in the Bahamas (~ 100 breeding pairs as of 2003, but numbers are much lower as of 2018; Mackin 2007; Iverson, Personal Observation). Before a year-long mouse eradication effort conducted in 2012 (Alifano et al. 2012), introduced house mice (first observed in 2003; Mackin 2007) and non-native barn owls attracted by access to the mice were present on Allen Cay. Owls expanded their diets to include shearwaters and consequently, partially consumed shearwater carcasses littered Allen Cay for at least 11 years (2007–2018; Mackin 2007; Iverson, Personal Observation). For example, new carcasses of 168 shearwaters were found on Allen Cay between December 2011 and May 2012 (Mackin, Personal Communication to Iverson). Mice carcasses were also observed on Allen Cay (Iverson, Personal Observation). Most of the iguanas on Allen Cay were transported to FRRC in May 2011 and 2012 to prevent their exposure to rodenticide (brodifacoum) used to eradicate the mice (Iverson 2012). Only two severely emaciated males were recovered in May 2013, suggesting most translocated individuals starved to death on FRRC. Only a few *C.c. inornata* that were not translocated to FRRC remain on Allen Cay.

Sample collection

We collected blood plasma and skin from *C. c. inornata* for stable isotope analysis in May of varying years from each cay (Table S1). We sampled plasma and/or skin from iguanas in 2011 and 2012 on Allen Cay (plasma, $n = 13$), in 2012 on FRRC (plasma, $n = 12$), and in 2013 on Leaf (plasma, $n = 23$; skin, $n = 91$) and U (skin, $n = 49$) Cays. We also collected samples of all potential iguana dietary items (as indicated by Hines 2011, 2013) in May 2013 from all cays using broad spatial sampling across each island (Table 2). We sampled molting skin when available from randomly caught individuals on each cay during mark and recapture surveys. On the one island where iguanas have access to food from tourists (Leaf Cay), we spread our trapping efforts across the cay to avoid oversampling individuals that frequent the tourist beach.

We drew blood samples from the caudal vein using heparinized syringes and stored the blood in cryovials in a cooler until the end of each collection day. We centrifuged blood then used a syringe to transfer plasma onto pre-combusted glass fiber filter papers where they were air-dried inside vials. The plasma collected in 2011 and 2012 was preserved in ethanol which has been shown to have no effect on the stable isotope values from vertebrate blood (Hobson et al. 1997; Therrien et al. 2011).

We collected both stems and leaves from plant species representative of those found in the diet of *C. c. inornata* on each cay (Table 2) (Hines 2013, 2016). Iguanas have occasionally been observed consuming invertebrates; so, we collected terrestrial and marine invertebrates when available (Table 2). We froze or pressed and dried all plant material immediately after collection. Invertebrates were kept alive for 48 h to clear gut contents, and then frozen at − 20 °C until prepared for analysis in the Kurle Lab at the University of California, San Diego. We used tissue from dried shearwater carcasses and mouse tail clippings stored in ethanol collected opportunistically on Allen Cay in 2007.

We washed all samples (except blood components) in deionized water to remove impurities, and then froze everything at − 20 °C before freeze-drying the samples. We scraped plasma from their filter papers, ground all samples into a fine powder by hand, and then weighed 0.5–1.0 mg and 3.0–4.0 mg of powder from animal and plant tissues, respectively, into 5 × 9 mm tin capsules for stable isotope analyses at the Stable Isotope Laboratory at the University of California, Santa Cruz. We calculated average precision as the SD of the $\delta^{13}C$ and $\delta^{15}N$ values from a set of standards (acetanilide) measured across all stable isotope runs, and they were 0.5‰ and 0.2‰, respectively. Iguanas on Leaf Cay had access to human food; so, we estimated the $\delta^{13}C$ and $\delta^{15}N$ values for human food using values reported for human hair (− 17.1‰ and 8.8‰, respectively) in Hopkins and Ferguson (2012; see their Table S3) corrected for isotopic discrimination using stable isotope discrimination factors ($\Delta^{13}C = 2.2$‰, $\Delta^{15}N = 2.9$‰) determined for hair from male and female rats held on known omnivorous diets from Kurle et al. (2014; see their Table 2).

Table 2 Mean $\delta^{13}C$ and $\delta^{15}N$ values (‰ ± SD) from potential iguana forage items on each cay in this study. All dietary items from Allen Cay had significantly higher $\delta^{15}N$ values than those from other cays. See text for details. FRRC is Flat Rock Reef Cay

Cay	Food item	$\delta^{13}C$	$\delta^{15}N$	*N*
Allen	C_3 plants[a]	− 26.2 ± 1.7	8.8 ± 3.7	72
	C_4 plants[b]	− 13.8 ± 0.9	10.6 ± 2.9	14
	Marine inverts[c]	− 20.1 ± 0.6	10.6 ± 0.6	3
	Mice[d]	− 18.8 ± 1.1	16.1 ± 1.2	6
	Shearwaters[e]	− 17.7 ± 0.8	8.6 ± 0.7	9
FRRC	C_3 plants	− 26.8 ± 1.8	1.6 ± 1.8	48
	C_4 plants	− 13.8 ± 0.3	2.2 ± 2.2	6
	Marine inverts	− 19.8 ± 0.7	3.2 ± 0.9	3
	Terrestrial inverts[f]	− 24.2 ± 0.3	5.1 ± 1.5	2
Leaf	C_3 plants	− 27.3 ± 1.6	− 0.5 ± 1.8	57
	C_4 plants	− 14.1 ± 0.4	4.9 ± 1.4	6
	Human food[g]	− 19.3 ± 0.8	5.9 ± 0.5	20
	Marine inverts	− 22.6 ± 0.9	3.8 ± 1.8	6
	Terrestrial inverts	− 25.4 ± 2.2	0.4 ± 2.0	10
U	C_3 plants	− 27.1 ± 1.6	− 0.8 ± 1.7	43
	C_4 plants	− 13.5 ± 1.0	1.3 ± 2.1	9
	Marine Invertebrates	− 19.8 ± 3.2	4.7 ± 2.1	7

[a]C_3 plants: *Borrichia arborescens, Bumelia americana, Casasia clusiifolia, Conocarpus erectus, Coccoloba uvifera, Drypetes diversifolia, Eugenia foetida, Guanicum sanctum, Ipomoea indica, Jacquinia keyensis, Leucothrinax morrisii, Manilkara bahamensis, Pithecellobium keyense, Rhachicallis americana, Solanum bahamense, Suriana maritima, Sesuvium portulacastrum,* and *Sophora tomentosa*

[b]C_4 plants: *Thalassia testudinum* and *Uniola paniculata*

[c]Marine invertebrates: crab, hermit crab, marine snail (muscle tissue), and Porifera (marine sponge)

[d]House mice (*Mus musculus*)

[e]Audubon's Shearwaters (*Puffinus iherminieri iherminieri*)

[f]Terrestrial invertebrates: Blattodea (cockroach), Coleoptera (beetle), Isoptera (termite), Lepidoptera (caterpillar), and Thysanura (silver fish). We used the $\delta^{13}C$ and $\delta^{15}N$ values from terrestrial invertebrates from FRRC for use in the stable isotope mixing model estimating iguana diets from U Cay as U Cay has a more similar bird-density (very low) to FRRC than to Leaf Cay (no birds)

[g]Human food stable isotope values were estimated using data from Hopkins and Ferguson (2012) and Kurle et al. (2014). See "Methods" for details

Statistical analyses

We calculated mean body mass (g) and snout–vent length (SVL; cm) of adult iguanas from each population using data collected during 2011 and 2012 from J. Iverson's long-term mark–recapture studies of *C. c. inornata* on our study islands (Iverson et al. 2004a, b). We used ANOVA and Tukey's posthoc tests to compare size data among islands. We used *t* tests or ANOVA and Tukey's Post hoc tests to compare the stable isotope values from skin and plasma collected from iguanas and from the different diet items between and among the cays. The $\delta^{13}C$ and $\delta^{15}N$ values were the same between paired skin (mean ± SD $\delta^{13}C = -24.0 \pm 0.7‰$ and $\delta^{15}N = 5.6 \pm 2.1‰$) and plasma (mean ± SD $\delta^{13}C = -24.2 \pm 0.7‰$ and $\delta^{15}N = 5.9 \pm 1.7‰$) collected from iguanas on Leaf Cay ($n = 15$; paired *t* tests, $p = 0.08$ and 0.48, respectively); therefore, all isotope values from skin and plasma collected on Leaf Cay were combined for comparison of iguana isotope values among the four cays. Skin was the only tissue sampled from iguanas on U Cay, but as we found no differences in isotope values between paired skin and plasma from iguanas on Leaf Cay, we used the isotope values from skin from iguanas on U Cay for comparison with isotope values from iguanas on all other Cays.

We used Systat 13 (Cranes Software International) for all statistical analysis, significance was tested at $\alpha = 0.05$, and all means are reported ± SD. We estimated proportions of iguana diet composed of C_3 plants, C_4 plants, invertebrates, and, where appropriate, mice, shearwaters, and human food, using MixSIAR (Stock et al. 2018), a Bayesian stable isotope mixing model incorporating mean (± SD) trophic discrimination factors for stable carbon and nitrogen isotopes ($\Delta^{13}C$ and $\Delta^{15}N$: blood, + 2.5 ± 0.6‰ and + 4.1 ± 0.4‰; Skin, + 4.5 ± 1.4‰ and + 6.0 ± 0.6‰) from adult Rock Iguanas (*Cyclura* spp.) (Steinitz et al. 2016), the $\delta^{13}C$ and $\delta^{15}N$ values from iguanas (Supplemental Table S1), and the mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values from their potential diet items (Table 2).

Results

Iguana size comparisons among cays

The mean SVL (cm) of iguanas varied among the cays (ANOVA, $F_{3, 375} = 69.85$, $p < 0.0001$) and iguanas from Allen Cay were ~ 1.7 times longer (48.3 ± 11.6) than those from the other cays (27.8 ± 4.9 to 28.8 ± 4.6) (Tukey's, $p < 0.0001$ for all comparisons). SVL did not vary across the other three cays (Tukey's, $0.55 \leq p$ 1.00; Fig. 2). Body mass (g) also differed among cays (ANOVA; $F_{3, 372} = 151.82$, $p < 0.0001$) and iguanas from Allen Cay were ~ six times heavier (5499 ± 2847) than those on other cays (914 ± 540 to 948 ± 743; Tukey's, $p < 0.0001$ for all comparisons). Body mass did not differ across the other three cays (Tukey's, $p \geq 0.99$; Fig. 2).

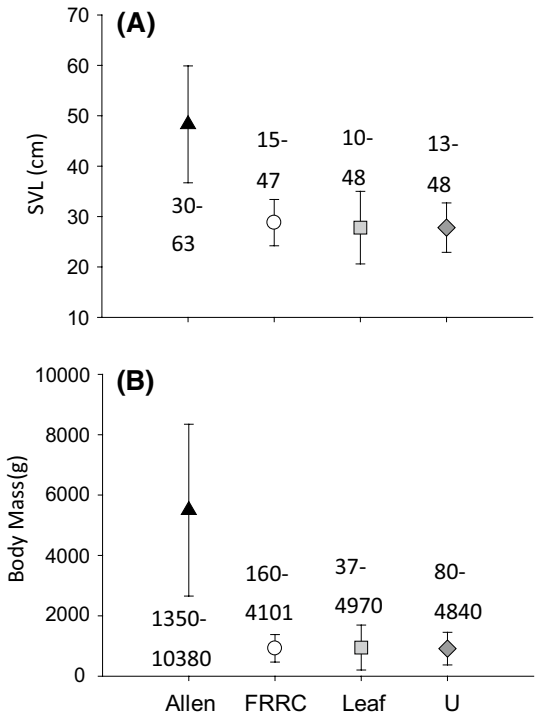

Fig. 2 The mean (± SD) **a** snout-ventral lengths (SVL, cm) and **b** body masses (g) for iguanas on Allen ($n = 18$), Flat Rock Reef (FRRC; $n = 209$), Leaf ($n = 77$), and U ($n = 75$) Cays. Numbers indicate the size ranges. Measurements were taken in 2011 and 2012, with no repeated individuals. The SVL and body mass were significantly higher for iguanas on Allen Cay vs. all other cays; there were no differences in body measurements from iguanas among other cays

Comparisons of stable isotope values from iguana tissues across islands

Due to the constraints of opportunistic sampling, we were unable to collect the same tissues for stable isotope analysis from all iguanas across all cays for all years. However, as the $\delta^{13}C$ and $\delta^{15}N$ values from paired skin and plasma samples collected from iguanas on Leaf Cay were the same (see "Methods"), we grouped the isotope values together for analyses and used the $\delta^{13}C$ and $\delta^{15}N$ values from skin samples from iguanas on U Cay as skin was the only tissue sampled on that Cay. To test for differences in iguana foraging ecology and the food web structure across islands, we compared the $\delta^{13}C$ and $\delta^{15}N$ values from iguana tissues among cays. Iguanas on Allen Cay had much higher $\delta^{15}N$ values (13.1 ± 1.0‰) than those from iguanas on all other cays (4.0 ± 1.4‰ to 5.5 ± 1.6‰) (ANOVA, $F_{3,161} = 100.6$, $p < 0.0001$; all Tukey's $p < 0.0001$). The $\delta^{15}N$ values from

iguanas on FRRC were not different than those on Leaf (Tukey's, $p = 0.965$) or U (Tukey's, $p = 0.158$) Cays, but iguanas on Leaf Cay had higher δ^{15}N values than those from U (Tukey's, $p < 0.0001$) (Table S1; Fig. 3). Iguanas on Allen Cay had lower δ^{13}C values (− 24.6 ± 0.5‰) than Leaf (− 24.0 ± 0.7‰) and U (− 22.9 ± 0.7‰) Cays but were the same for iguanas on FRRC (− 24.5 ± 0.5‰). All other inter-island comparisons of the δ^{13}C values from iguanas were different (Tukey's, all $p < 0.05$) (Table S1; Fig. 3).

Comparisons of stable isotope values from potential dietary items across islands

The δ^{15}N values from the C_3 plants were significantly higher on Allen Cay than on any other cay (ANOVA; $F_{3, 216} = 194.16$, $p < 0.01$; Tukey's, all $p < 0.01$) (Fig. 3; Table 2). The δ^{15}N values from the C_3 plants on FRRC were higher than those from Leaf and U Cays (Tukey's, $p < 0.01$), but there were no differences in the δ^{15}N values from the C_3 plants on Leaf and U Cays (Tukey's, $p = 0.97$). The δ^{13}C values from the C_3 plants differed among the cays (ANOVA; $F_{3, 216} = 4.72$, $p < 0.01$), and those from Allen Cay were higher than those on Leaf and U Cays (Tukey's, $p < 0.01$ and $p = 0.03$, respectively). The δ^{13}C values from the C_3 plants on FRRC did not differ from those on the other cays (Tukey's, $0.27 < p < 0.97$).

The δ^{15}N values from the C_4 plants were significantly higher on Allen Cay than on any other cay (ANOVA; $F_{3,31} = 33.55$, $p < 0.01$; Tukey's, all $p < 0.01$). The δ^{15}N values from the C_4 plants on Leaf Cay were higher than those on U Cay (Tukey's, $p = 0.04$), but values from FRRC did not differ from those on Leaf or U Cays (Tukey's; $p = 0.23$ and $p = 0.90$, respectively). There were no differences in the δ^{13}C values from the C_4 plants among islands (ANOVA; $F_{3,31} = 0.76$, $p = 0.53$) (Fig. 3; Table 2).

The δ^{15}N values from the marine invertebrates were significantly higher on Allen Cay than on any other cay (ANOVA, $F_{3,15} = 12.7$, $p < 0.01$; Tukey's, all $p < 0.01$), whereas they did not differ among FRRC, Leaf, and U Cays (Tukey's, $0.6 < p < 0.9$). There were no differences in the δ^{13}C values from the marine invertebrates among islands (ANOVA, $F_{3,15} = 2.36$, $p = 0.11$). Mean δ^{13}C values from terrestrial invertebrates opportunistically collected from FRRC and Leaf Cays did not differ (t test, $p = 0.49$), but mean δ^{15}N values from FRRC were higher than those from Leaf Cay (t test, $p = 0.01$) (Fig. 3; Table 2).

Shearwaters and mice were only available as potential prey on Allen Cay and their mean δ^{13}C values were much higher than those from iguanas on Allen and all other cays (Fig. 3; Table 2), whereas the δ^{15}N values from shearwaters were much lower than those from mice and almost identical to the C_3 plants on Allen Cay. Human food items were available to iguanas from tourists on Leaf Cay, and the mean δ^{13}C and δ^{15}N values estimated for these items fell within the range of the other diet items on the cay (Fig. 3; Table 2).

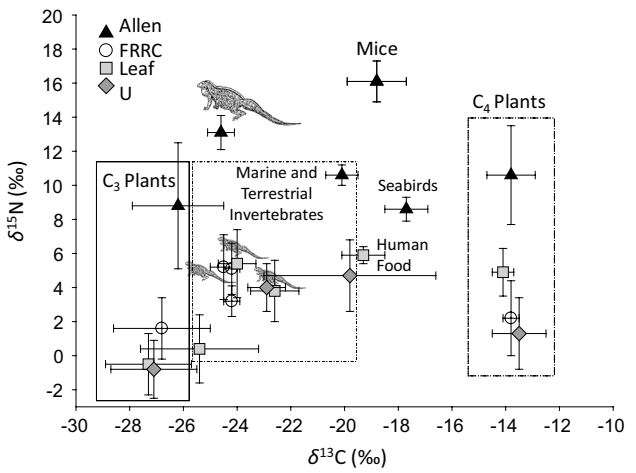

Fig. 3 The mean (± SD) stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values from plasma and skin collected from Allen Cay rock iguanas across the four study islands [Allen ($n = 13$ plasma samples), Flat Rock Reef (FRRC; $n = 12$ plasma samples), Leaf ($n = 23$ plasma and 68 skin samples), and U ($n = 49$ skin samples) Cays] along with values from potential iguana diet items collected from Allen, Flat Rock Reef, Leaf, and U Cays

%N in plant tissues among cays

Leaves from plants on Allen Cay contained nearly twice as much nitrogen (1.9 ± 1.0%) as leaves from the other cays (1.0 ± 0.4% to 1.2 ± 0.5%; ANOVA, $F_{3, 142} = 16.57$, $p < 0.01$; Tukey's, $p < 0.01$ for all comparisons), whereas there were no differences in the %N in leaves among plants from the other cays (Tukey's, all $p \geq 0.46$) (Fig. 4). Similarly, stems of plants from Allen Cay contained nearly twice as much nitrogen (1.8 ± 1.0%) as those from the other cays (1.0 ± 0.4% to 1.1 ± 0.5%; ANOVA, $F_{3, 96} = 11.58$, $p < 0.01$; Tukey's, $p < 0.01$ for all comparisons), but there were no differences in %N in stems from plants collected on the rest of the cays (Tukey's, all $p \geq 0.96$) (Fig. 4).

Iguana foraging ecology

The estimated assimilated diets of iguanas across all islands were largely composed of C_3 plants (means 74.0–97.7%), with very little to no input from C_4 plants (means < 3.2%), human food (only available on Leaf Cay; mean < 3.7%), marine invertebrates (means < 7.1%), and mice or shearwater carcasses (only available on Allen Cay; means 2.2% and 2.6%, respectively). Iguanas may have been consuming terrestrial invertebrates in measurable, but small, quantities on Leaf Cay (means from 11.9 to 17.0%) (Table 3).

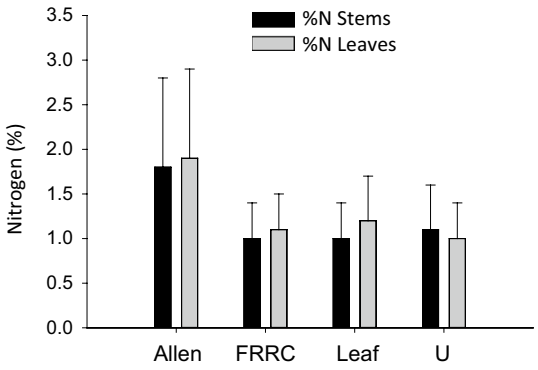

Fig. 4 The nitrogen content (%) of stems and leaves from plants on Allen ($n=33$, 48), Flat Rock Reef (FRRC; $n=20$, 30), Leaf ($n=24$, 34), and U ($n=23$, 34) Cays

Discussion

We used stable isotope analysis of iguana tissues and their food sources, along with nutrient data from plants, to investigate the potential that the population of *C. c. inornata* on Allen Cay had grown 1.7 times longer and nearly six times heavier than their conspecifics on three nearby Bahamian islands due to their unique access to (1) animal prey (mice and/or shearwaters) and/or (2) higher-quality food sources with increased nutrients derived from marine subsidies. As outlined above, Allen Cay is the only island in this study that contained invasive mice, and that still supports a large, though declining, breeding population of Audubon's Shearwaters (Lee 2000; Mackin 2007). The mice on Allen Cay attracted non-native barn owls from nearby sources (likely Highborne Cay), which also targeted shearwaters. Depredation of shearwaters by barn owls left carcasses with abundant tissue for potential carrion feeding by iguanas. Despite this, results from the Bayesian stable isotope mixing models (Table 3) provided no support for the hypothesis that iguanas

Table 3 Proportional dietary contributions for Allen Cays Rock Iguanas sampled on Allen, Flat Rock Reef (FRRC), Leaf, and U Cays in the Bahamas, 2011–2013

Source	Island	Year	Tissue	*N*	Population level		Credible interval		
					Mean	1 SD	2.5%	50%	97.5%
C_3 plants	Allen	2011/12	Plasma	13	89.7	7.6	69.0	92.2	98.0
	FRRC	2012	Plasma	12	92.9	4.0	82.8	93.7	98.2
	Leaf	2013	Plasma	23	75.4	5.0	65.3	75.4	85.0
	Leaf	2013	Skin	91	97.7	1.1	95.4	97.8	99.5
	U	2013	Skin	49	97.7	1.3	94.3	97.9	99.5
C_4 plants	Allen	2011/12	Plasma	13	1.3	1.7	0.1	0.8	5.2
	FRRC	2012	Plasma	12	1.0	0.9	0.0	0.7	2.8
	Leaf	2013	Plasma	23	0.9	0.9	0	0.6	3.4
	Leaf	2013	Skin	91	0.3	0.3	0	0.2	1.1
	U	2013	Skin	49	0.6	0.6	0	0.3	2.3
Human food	Leaf	2013	Plasma	23	2.6	2.0	0.2	2.1	7.1
	Leaf	2013	Skin	25	0.4	0.4	0	0.2	1.5
Marine invertebrates	Allen	2011/12	Plasma	13	4.3	5.3	0.1	2.4	22.4
	FRRC	2012	Plasma	12	2.0	1.6	0.1	1.5	6.0
	Leaf	2013	Plasma	23	5.2	3.5	0.5	4.5	13.6
	Leaf	2013	Skin	91	0.7	0.5	0	0.5	2.0
	U	2013	Skin	49	0.7	0.7	0	0.4	2.6
Mice	Allen	2011/12	Plasma	13	2.2	2.3	0.1	1.3	8.5
Shearwaters	Allen	2011/12	Plasma	13	2.6	3.7	0.1	1.5	15.5
Terrestrial invertebrates	FRRC	2012	Plasma	12	4.2	4.0	0	2.9	14.1
	Leaf	2013	Plasma	23	16.0	6.1	4.5	15.5	28.8
	Leaf	2013	Skin	91	1.0	0.9	0	0.7	3.2
	U	2013	Skin	49	1.1	1.0	0	0.7	4.0

Parameters were estimated by the Bayesian stable isotope mixing model MixSIAR. Source availability varied by island: mice and shearwater carcasses were only found on Allen, human food was only on Leaf, and we did not have terrestrial invertebrate data for Allen. The model outcomes indicate C_3 plants dominated the diets of iguanas on all islands

on Allen Cay were eating mice or shearwaters. Rather, iguanas on all cays appear to be eating almost exclusively C_3 plants, the $\delta^{15}N$ values from plants on Allen Cay were two–three times higher than those from all other islands, and the nutrient contents (%N) of plants on Allen Cay were nearly twice that of plants on the other islands (Tables 2 and 3; Figs. 3 and 4).

Plant species composition is similar among all four study islands (Alifano et al. 2012; Iverson et al. 2004a), but Allen Cay has been recorded as having slightly greater diversity, lower canopy height, and reduced tree cover compared to Leaf, U, or Flat Rock Reef Cays (Alifano et al. 2012). These subtle differences in plant communities, potentially augmented by marine subsidy inputs on Allen Cay, could have made plants more easily accessible for foraging by the larger-bodied iguanas on Allen Cay, and increased food abundance and availability has been thought to contribute to larger body size of some insular mammals (Raia and Meiri 2006) and marine iguanas (Chiari et al. 2016). However, that does not explain the elevated $\delta^{15}N$ values measured from the iguanas, the plants, and all other potential diet items on Allen Cay compared to those from all other cays, along with the elevated nitrogen content.

Marine-derived nitrogen has higher $\delta^{15}N$ values than terrestrial-derived nitrogen (Caut et al. 2012) and seabird guano subsidies deposited on islands, especially by high-trophic level consumers with elevated $\delta^{15}N$ values, such as shearwaters, should lead to a terrestrial food web whose members exhibit significantly higher $\delta^{15}N$ values (Anderson and Polis 1999) than those on islands without marine-derived guano subsidies. In keeping with our second mechanistic hypothesis, this is exactly what we observed. All components of the food web on Allen Cay exhibited $\delta^{15}N$ values ~ 5 to 9‰ higher than those on the other cays (Fig. 3; Table 2), and these higher values are characteristic of seabird guano inputs (Barrett et al. 2005; Croll et al. 2005; Fukami et al. 2006; Jones 2010; Maron et al. 2006; Szpak et al. 2012). In addition, the $\delta^{15}N$ values of the iguanas compared with those from the mice and shearwaters (Fig. 3) do not suggest any ^{15}N-enrichment associated with their consumption of mice or birds. Thus, the higher $\delta^{15}N$ values observed in iguanas from Allen Cay compared with those from the other cays likely does not represent a shift in foraging behavior of Allen Cay iguanas toward more carnivory, but rather supports our hypothesis that iguanas utilize C_3 plants with higher $\delta^{15}N$ values derived from marine subsidies in the form of shearwater guano deposition.

Iguanas are limited in the amount of forage they can ingest and process in a given time period. For example, the presence of colic folds in largely herbivorous iguanas is thought to increase absorptive surface area, provide microhabitats for microbes that aid in the breakdown and fermentation of plant material, and slow the movement of food for increased digestive action (Iverson 1980; Mackie et al. 2004). Therefore, the near doubling of the nitrogen content we measured in plants on Allen Cay (Fig. 4) would, thus, translate into greater growth potential for the iguanas on Allen Cay as they likely absorb more nutrients per unit time than their conspecifics on islands with lower nutrient quality plants and supports our hypothesis that high nutrient density is driving large body size in these iguanas.

In addition, very high rates of nutrient transport from marine into terrestrial ecosystems is frequently linked to increased primary and secondary production (Caut et al. 2012; Farina et al. 2003; Gillham 1960; Polis et al. 1997; Polis and Hurd 1996), and increases in clutch and body sizes of other insular reptiles have been directly correlated with the increased marine subsidies that drive this higher production (Pafilis et al. 2009, 2011). For example, geckos (*Lepidodactylus* spp.) in seabird-subsidized forests were larger and had significantly higher body condition than geckos in non-subsidized systems (Briggs et al. 2012). Finally, an increase in nitrogen concentration of food sources has been attributed to larger clutch sizes, larger body sizes, and increased growth rates in reptiles (Briggs et al. 2012; Pafilis et al. 2009, 2011). Nitrogen addition can also cause the accretion of free amino acids in plants, potentially contributing to increased herbivore growth through consumption of these easily digestible and frequently inadequately supplied nitrogen compounds (Strengbom et al. 2002; White 1993).

Small differences in the $\delta^{13}C$ and $\delta^{15}N$ values across iguanas originating on FRRC, Leaf, and U Cays may reflect differential consumption of terrestrial invertebrates and human food (on Leaf Cay). For example, the slightly higher $\delta^{15}N$ values from skin from iguanas on Leaf vs. U Cay could reflect human food consumed by some iguanas on Leaf Cay. The stable isotope values from skin and plasma collected from iguanas on Leaf Cay were the same, despite the fact that each tissue has a different protein turnover rate and thus different isotope incorporation rates (Kurle 2009; Reich et al. 2008). This indicates that, regardless of the time period during which the isotope values were incorporated into the tissues, the iguana diets remained relatively consistent. The presence or absence of seabird guano is not expected to greatly change the $\delta^{13}C$ values of terrestrial soil or vegetation (Mizutani and Wada 1988) because C_3 plants contribute the most to soil organic matter, even on islands with seabird colonies (Mizutani and Wada 1988). Thus, it is not clear why C_3 plants from Allen Cay had slightly higher $\delta^{13}C$ values than those from Leaf and U cays. However, marine-derived carbon is enriched in ^{13}C compared to the carbon in C_3 plants (~ − 17.0‰ for marine algae vs. ~ − 27.0‰ for terrestrial, C3 plants); so the small amount of guano-derived carbon that may contribute to terrestrial soil nutrients could slightly increase the $\delta^{13}C$ values of the plants on Allen Cay. In addition, the slightly higher $\delta^{15}N$ values from C_3 plants

and terrestrial invertebrates on FRRC could be due to small guano inputs from its very low density of gulls.

We recognize that a sample size of one island with seabirds vs. three without is small, and an unavoidable consequence of collecting comparative data of this type given the limited natural experiment opportunities presented by an endangered species inhabiting only a few small islands. However, important ecological inferences have been made using small sample sizes of islands with and without certain parameters. For example, Onuf et al. (1977) collected island recolonization rate data on one far-from vs. three nearer-to faunal source islands to illuminate the theory of species equilibrium and Simberloff and Wilson (1970) compared one seabird-containing vs. one seabird-free mangrove covered islands to assess the role of nutrients from seabirds on mangrove growth rates. Therefore, we are confident that the data we collected on one vs. three islands are adequate to support our proposed mechanism.

In conclusion, by comparing islands with and without seabird-driven marine subsides, interisland differences were revealed in both the body size of iguana populations and in the insular food web structure. Marine-derived subsidies from seabird guano on Allen Cay caused an increase in %N in the plants and a resultant increase in the δ^{15}N values across the entire food web relative to non-seabird islands. The increase in nutrient availability on seabird islands through marine-derived nitrogen inputs facilitated more nutrient-rich vegetation and allowed for increased growth and significantly larger-bodied iguanas. Whether this mechanism explains the significant body size variation observed among island populations of other West Indian iguanas (*C. c. figginsi and C. rileyi*) (Hayes et al. 2004; Knapp and Hines 2006) remains to be studied.

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Author contribution statement KMR, JBI, and CMK conceived of and designed the experiments, KMR and JBI collected the data in the field in the Bahamas, KMR did the laboratory work, KMR and CMK analyzed the data, and KMR, JBI, and CMK wrote and edited the manuscript.

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